THE F_1 BLEND ACCOMPANIED BY GENIC PURITY

A Description of Mechanical Charts for Illustrating Mendelian Heredity in Each of Three Well-known Cases of Blending Inheritance in the First Hybrid Generation

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The mechanical charts herewith figured are the first of a series prepared for the purpose of presenting graphically and schematically the established facts of heredity. These particular mechanisms, illustrating blending inheritance, consist essentially of wooden slabs on which the gametic formulæ of the several generations are charted —those for P_1 and F_2 are written on flat surfaces, while that for F_1 is inscribed on cylinders which turn freely. A capital letter represents a gene; the corresponding small letter the absence of that gene. The location of genes, whether they lie in the same chromosome *i. e.,* are linked, or in different chromosomes, is shown graphically by placing their symbols in the same or in different squares, or upon the same or different half-cylinder surfaces. In each of these selected cases the individuals of the P_1 generation are homozygous in respect to both of the traits or allelomorphic phases concerned. The genes contributed by the P_1 generation to the F_1 zygote are charted on the starred faces of the freely turning cylinders. The back of each spool contains the same inscription as the face of its partner cylinder. Each face of a cylinder represents a chromosome—the two faces the two chromosome types in reference to the

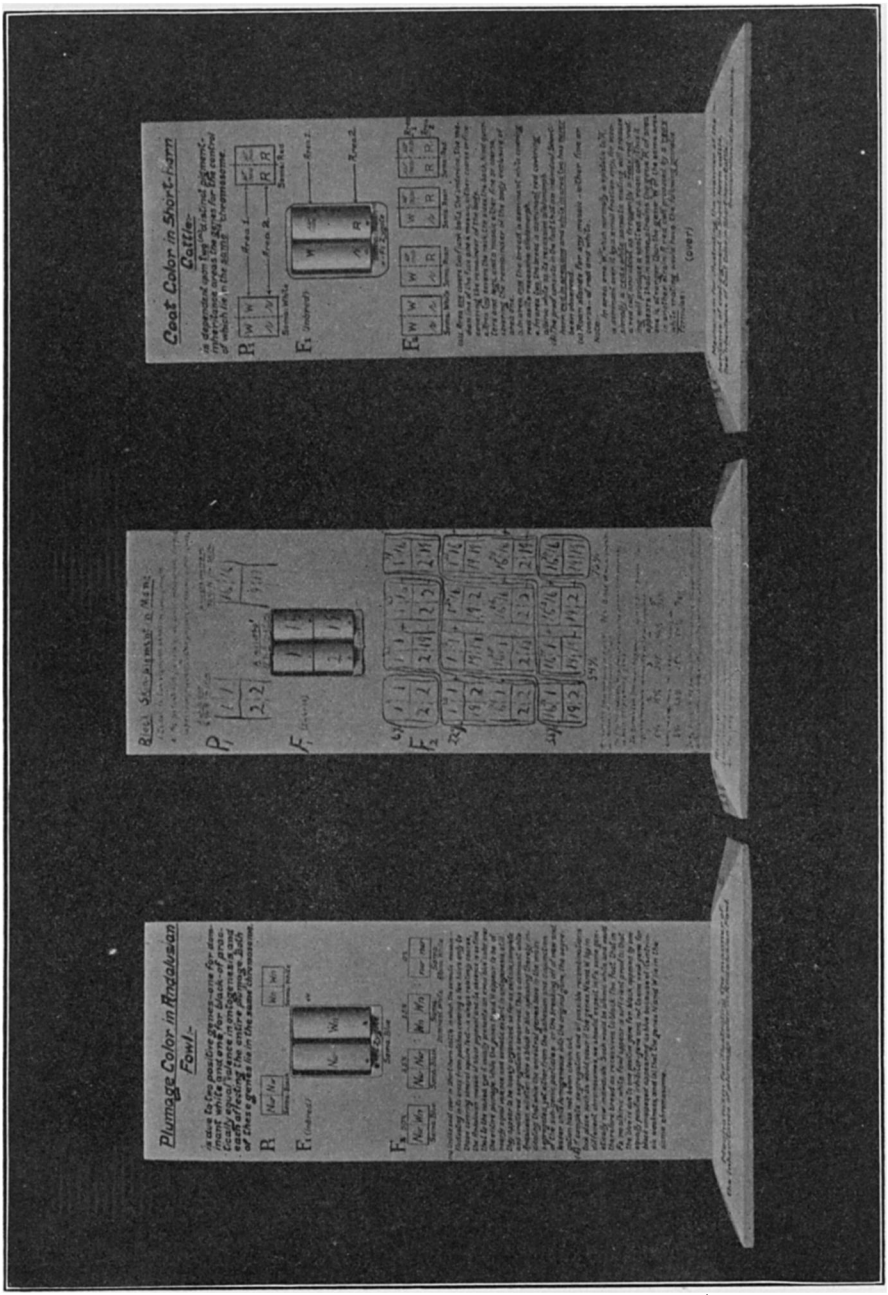

FIG. 1. Three Mechanical Charts demonstrating Mendelian Processes in Cases of Blending Inheritance

traits lying in that particular chromosome, which each F_1 individual as a parent is capable of passing on. Therefore, by turning the spools so that all possible combinations are made, one can read off directly all of the different hereditary potentialities to be had by inbreeding the F_1 generation. Consequently the F_2 line (which is charted on a flat surface) is simply a record of such combinations.

For the purpose of this study a case of blended inheritance is one in which the development in F_1 of a given somatic trait—regardless of whether it develops from one or more genes—is about midway between its development in the two parents, each of which is of pure stock in reference to the trait concerned. Until about the year 1910 students of heredity were unable to coordinate the general rule of dominance and segregation on one hand, with the frequent exception of blending and segregation on the other. Now the existence of at least three different routes by each of which nature arrives at the somatic blend in F_1 are recognized, and each finds ready interpretation in consonance with the theory of the pure gene. The first of these is the dilution or true blend route, by which nature appears to travel in the classical cases of the Blue Andalusian[1] fowl resulting from the crossing of splashed-white and black parents, and of the pink four o'clock (*Mirabilis jalapa*) resulting from the crossing of red and white parents.

The ordinary mode of inheritance is strongly duplex—that is, the zygote normally possesses two genes for each trait, either one of which genes is usually sufficient—with possibly a liberal surplus of valence—to give full somatic expression to its correlated trait. In such cases complete dominance in F_1 and clear-cut segregation in F_2 are the rule. Occasionally, however, in cases wherein a duplex parent possesses a strong somatic development of a trait,

[1] "Mendel's Principles of Heredity" (3d Impression, 1912), p. 51, by W. Bateson.

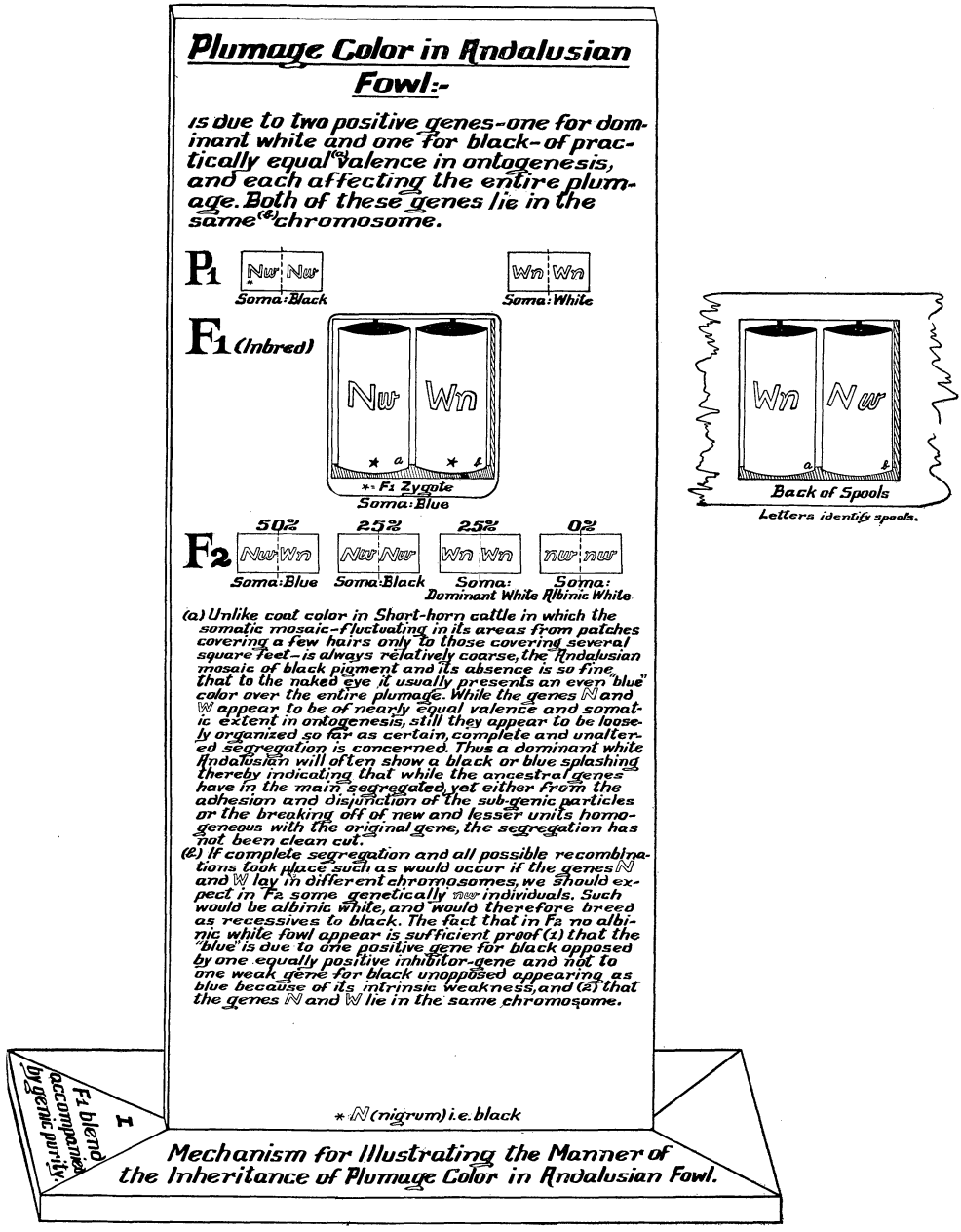

FIG. 2. Chart showing the F_1 Blend Associated with Genic Dilution—the True Blend

a single gene—from the paternal or the maternal line only—for such trait, in the zygote, is not sufficient to give a somatic development of the trait equal to that possessed by the duplex parent. In such cases, therefore, the unit trait in question is blended in the F_1 soma—a case of imperfection of dominance.[2] Nevertheless, in such cases segregation is just as clean-cut in the germ-plasm as it is in the cases accompanied by strong somatic dominance.

In Andalusian fowl "W"—dominant splashed-white—and "N"—(nigrum) black—are two opposing and allelomorphic genes of nearly equal valence in ontogenesis. Their combination and interaction determine plumage-color in the offspring. The black Andalusian is duplex for black plumage-pigment, while the splashed-white is duplex for dominant splashed-white. The F_1 offspring are "blue"—a shade really intermediate between the white and the black. Moreover, the genes "W" and "N" evidently lie in the same[3] chromosome. The evidence for this consists in the fact that in the F_2 generation, resulting from inbreeding two blue Andalusians, neither albinic white nor jungle[4]—pure or modified—patterned fowl result, which would be the case if "N" and "W" lay in different chromosomes, permitting, in some F_2 zygotic combinations, the elimination of both "N" and "W." For further explanation of this particular type of blended inheritance see the accompanying figure descriptive of the mechanical chart "Plumage-Color in Andalusian Fowl."

The second type—that of multiple factors—is typified by the inheritance of black skin-pigment in man. It is a matter of common knowledge that a mulatto of the first generation is about intermediate in density of black skin-pigment between his white and his black parents. In 1913

[2] "Imperfection of Dominance," *American Breeders Magazine*, No. 1, Vol. 1, p. 39, 1910, by C. B. Davenport.

[3] "Heredity and Sex," p. 93 et seq. (Columbia University Press, 1913), by Thomas H. Morgan.

[4] "New Views about Reversion," *Proceedings of the American Philosophical Society*, Vol. XLIX, No. 196, 1910, by C. B. Davenport.

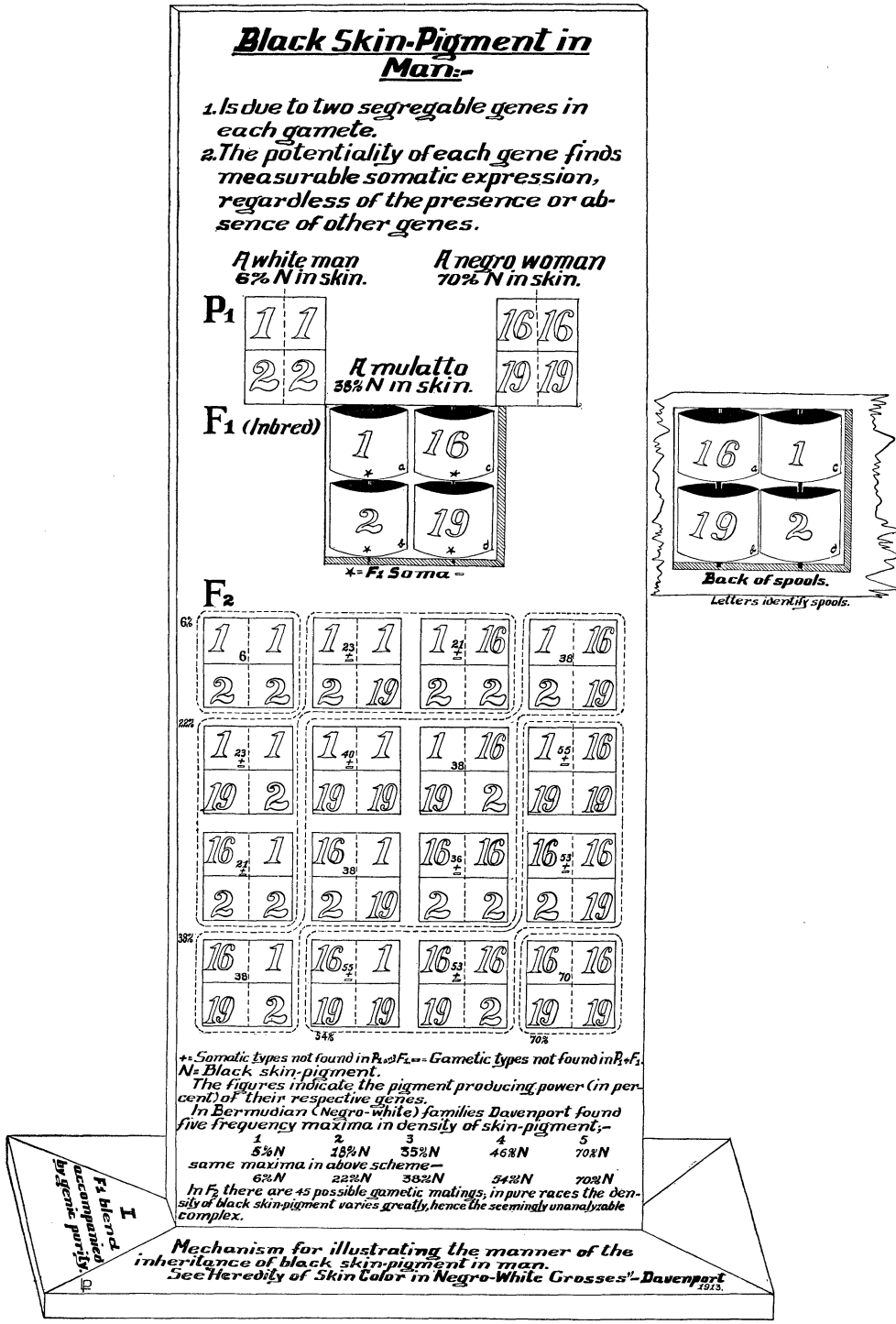

FIG. 3. Chart showing the F_1 Blend Associated with Multiple Factors for One Somatic Trait

Dr. C. B. Davenport[5] found, by analyzing data on the family distribution of black skin-pigment measured quantitatively (by the color-top) among the mixed white-and-black families of the Island of Jamaica, the Island of Bermuda, and in our own Southern States, (1) that black skin-pigment in man is the somatic working out of two segregable genes in each gamete, and (2) that the potentiality of each gene finds definite measurable somatic expression, regardless of the presence or absence in the zygote of other genes. Now these two genes appear to be of different valence; they appear also to lie in different chromosomes. The scheme outlined by the mechanical chart "Black Skin-Pigment in Man" is quite consonant with the facts of inheritance which Dr. Davenport found in nature. The facts seem to be that in white persons one of these genes will develop from practically none to about 1 per cent. of blackness in skin-color, and the second from very little to about 2 per cent., thus resulting in a blackness of skin-color of 6 per cent. or less in the somas of members of the light races. He found that some races of negroes show about 70 per cent. black in skin-color. In such races one gene for black skin-color seems to be potential to developing approximately 16 per cent. of black skin-color, the other about 19 per cent. The evidence that there are two such genes, and that they are segregable, *i. e.*, that they lie in different chromosomes, and that their values among the strains studied are about as described above, lies in the fact that, in the hybrid families in Bermuda, Davenport found 5 frequency maxima in intensity of black skin-pigmentation, and that his analysis of the family distribution of this trait, quantitatively measured in many mongrel families of known pedigree, demanded the existence in nature of the scheme above outlined.

Darwin, whose method of study was essentially observational, knew that the F_1 generation was quite generally

[5] "Heredity of Skin-Color in Negro-White Crosses," published by the Carnegie Institution of Washington, 1913, by Charles B. Davenport.

remarkably uniform, but among and beyond the F_2 general observation found no rule of inheritance. It remained for the application of the analytical or Mendelian study to discover order in the apparent somatic tangle of F_2. The skin-color story just related is a striking case in point.

The third class of blended inheritance—the particulate or mosaic—is typified by the behavior in heredity of coat-color in short-horn[6] cattle in which, in the F_1 soma, the

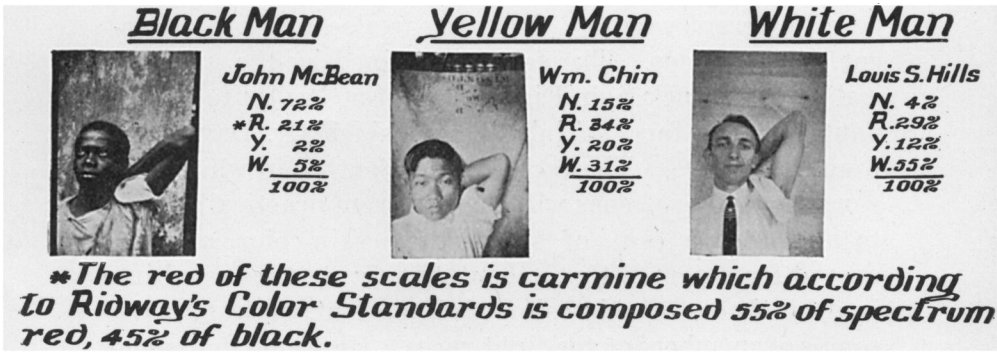

FIG. 4. Composition of Skin-pigmentation in Representatives of Three Races.

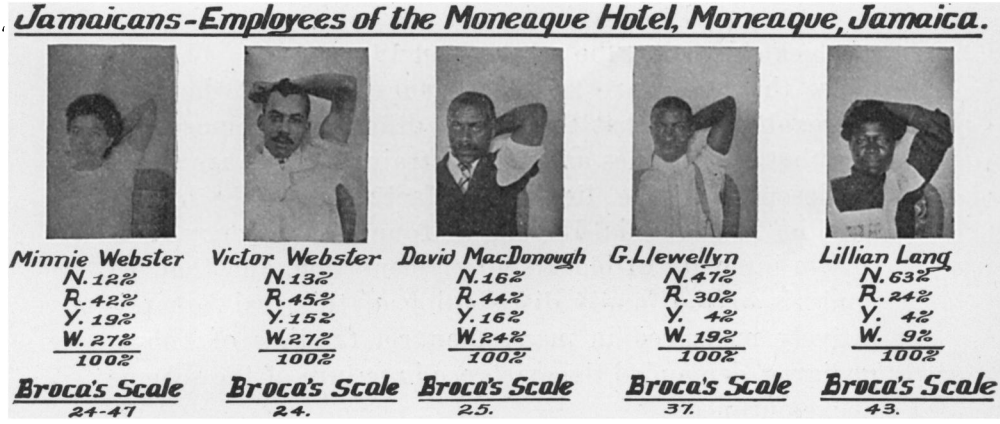

FIG. 5. Variation in Skin-pigmentation Among Jamaicans

[6] "Inheritance of Coal-Color in Short-horn Cattle," AMERICAN NATURALIST, December, 1911, January, 1912, by H. H. Laughlin.

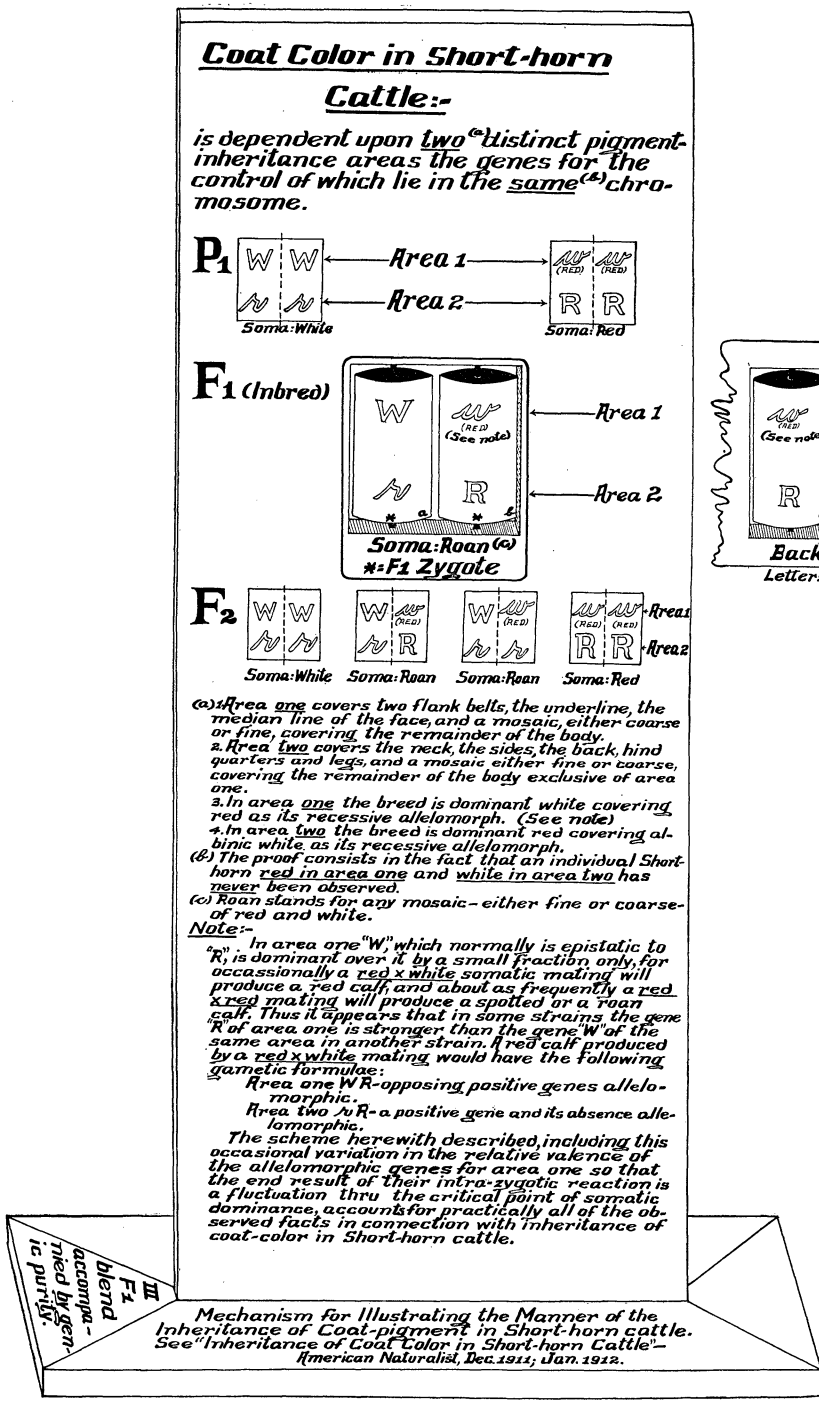

FIG. 6. Chart showing the F_1 Blend Associated with Particulate Inheritance—a Patent Mosaic

character concerned is, in its grosser aspect, clearly midway between the corresponding traits of its two parents, although a closer inspection reveals a mosaic the elements of which are the parental traits quite unchanged. The difference between the Andalusian fowl and the short-horn cattle cases seems to be as follows: In the Andalusian each gene influences the entire plumage-color, and appears to be struggling unsuccessfully, as it were, for the supremacy in somatic expression, thus resulting in a very fine and quite generally distributed blend or mosaic; while in short-horn cattle the controlling genes are double the number, each pair being confined to specific coat areas in somatic expression, and the resulting mosaic, although quite variable in coarseness, is always relatively coarse and is also quite definitely patterned.

Thus, normally (for the exception see the note in Fig. 6) in Area 1 the gene "W" is clearly dominant over the gene "R." In Area 2 the gene "R" is dominant over its absence. There seems to be in Area 2 no competing or allelomorphic gene whatever—it is simply "R" or its absence, *i. e.*, albinic white; whereas in Area 1 the "W," which is epistatic to "R," will leave "R" by its absence. The evidence for all this consists in the fact that a *white short-horn* (which is evidently dominant white, always duplex, in Area 1, and always recessive white in Area 2) will, when crossed with a black Angus, which is *dominant black for its entire coat,* give in the offspring a calf *dominant white, simplex, in Area 1,* and *black, simplex, in Area 2*—the familiar "blue roan" in cattle. That in short-horn cattle the genes "W" and "R" lie in the same chromosome is sufficiently proved by the fact that the color pattern is *never* reversed, that is to say, in *bi-colored individuals of whatever coarseness of mosaic, Area 1 is*

(Note:—When this paper on coat-color was written it was pointed out that coats red in Area 1 and white in Area 2 were *never* observed. Now the modified interpretation, involving linkage and a variation in genic valence, as explained in the text and Fig. 6 of the present article, accounts for practically all of the observed facts.)

always dominant white, and Area 2 is always red, and we never find an individual red in Area 1 and white in Area 2, although solid whites and solid reds, and bi-colored individuals of the first specified type are common. The reversed pattern, *i. e.*, red in Area 1 and white in Area 2, would occur if the genes "W" for Area 1 and "R" for Area 2 were completely segregable, *i. e.*, if they lay in different chromosomes. For a further explanation of this mode of blending inheritance see the accompanying chart, "Coat-color in Short-horn Cattle."